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OF THE

SOCIETY FOR BRITISH ENTOMOLOGY

World List abbreviation: *Trans.Soc.Brit.Ent.*

EDITED BY
J. H. MURGATROYD, F.L.S., F.Z.S., F.R.E.S.

WITH THE ASSISTANCE OF

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W. H. T. TAMS

DATE OF PUBLICATION: 16TH JULY, 1952

Copies may be purchased from the Secretary at 454 Christchurch Road, Bournemouth, Hants.

Price 5s. 0d. post free

SOCIETY FOR BRITISH ENTOMOLOGY

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DATES OF PUBLICATION OF PARTS

Part 1 (pp. 1-16) ..... 22nd August, 1951
Part 2 (pp. 17-80) .....31st October, 1951
Part 3 (pp. 81-96) ..... 6th December, 1951
Part 4 (pp. 97-124).....16th May, 1952
Part 5 (pp. 125-140) ..... 16th July, 1952
Part 6 (pp. 141-152) ..... 4th November, 1952
Part 7 (pp. 153-164) ..... 4th November, 1952
Part 8 (pp. 165-180) ..... 4th November, 1952
Part 9 (pp. 181-208) ..... 24th March, 1953
Part 10 (pp. 209-228) ..... 11th September, 1953
Part 11 (pp. 229-244) .....14th July, 1954
Part 12 (pp. 245-280) ..... 15th November, 1954

CORRIGENDA

Page 214. Line 15 from top. For "*Eubria*" read "*Eburia*".

Page 266. Line 24 from top. For "De Geer" read "Degeer".

Page 266. Line 8 from bottom. For "scots pine" read "Scots pine".

Page 268. Line 2 from top. For "scots pine" read "Scots pine".

Page 268. Line 4 from bottom. For "scots pine" read "Scots pine".

Page 274. Lines 27-28 from top. For "Scotch fir" read "Scots pine".

Page 274. Line 7 from bottom. For "Scotch fir" read "Scots pine".

Part 12. Inside Back Cover. Officers and Council. For 1953-4 read 1954-5.

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SYDENHAMS, PRINTERS, BOURNEMOUTH

TRANSACTIONS OF THE SOCIETY FOR BRITISH ENTOMOLOGY

VOL. 11 16TH JULY, 1952 PART 5

THE NATURAL HISTORY OF SOME *PAMPHILIUS* SPECIES (Hym., Pamphiliidae)

By V. H. CHAMBERS, Ph.D., A.R.C.S.

Hitherto most of the fourteen species of sawflies belonging to the genus *Pamphilius* have been regarded as being rare in Great Britain, records are scanty and little has been contributed upon their biology. The larvae are very distinct: firstly, on account of their unusual form, with their long eight-segmented antennae, the absence of abdominal legs and for the conspicuous projecting lateral appendages of the apical abdominal segment; secondly, in their mode of life of feeding more or less concealed in an abode constructed by rolling up and securing with threads a leaf or leaves of their food-plant. For our present knowledge of the biology of *Pamphilius* we are indebted to a great extent to the work of W. Stritt carried out in South Germany, published in a number of papers, of which that of 1935 (Stritt, 1935) is the most comprehensive. In recent years I have been fortunate in finding both the adults and larvae of a number of species, the latter sometimes in considerable numbers, and have been able to follow their development and to breed the adults. As the larvae have so rarely been recorded by entomologists in Britain it is probable that we are at present in a period of maximum abundance, cyclic alternations of great abundance and extreme scarcity being well known even with some of the so-called common species of sawflies. The following observations are presented as, in addition to Stritt's papers possibly not being easily accessible in Britain, they supplement his work in detail and include some new material.

Stritt, (1935) distinguished three types of larval abode or roll which he regarded as a better guide in the recognition of a species than a description of the larva, as the range of variation in colour of the latter overlapped the species. His definitions of these may be translated as follows:

(a) the larva draws up a leaf into an open trough or an enclosed tube or spins several leaves loosely together to enclose a hollow. A more or less complete tube of webbing is sometimes found within this abode.

(b) a wide marginal strip of the leaf is separated and rolled into a cone. In this way the narrow end of the cone remains directed towards the mid-rib of the leaf, the expanded part facing outwards. The cone is open at both ends. Intermediates between (a) and (b) often occur.

(c) the larva rolls a narrow, separated marginal strip of the leaf into a screw-like tube. Contrary to type (b), in this case the wider part of the roll —which is also that last constructed—is directed towards the centre of the leaf, the narrower part being distal and closed at the apex.

In the British fauna it now appears that type (b) is most frequent, being found in eight species, i.e., *betulae* L., *latifrons* Fallen, *vafer* L., *gyllenhali* Dahlb., *varius* Lep., *pallipes* Zett., *hortorum* Klug, and *fumipennis* Curt.; type (a) being characteristic of *sylvaticus* L., and *stramineipes* Hartig; type (c) of *inanitus* Vill. and *histrio* Latr., while in the remaining species *balteatus* Fallen and *sylvarum* Steph., the larval roll is undescribed. I have bred adults from the following type (b) larvae: two of the aspen species, *betulae* and *latifrons*; both birch species *varius* and *pallipes*; *gyllenhali* (*Salix*) and *vafer* (*Alnus*). Of these the larva and roll of *latifrons* is hitherto undescribed; Conde (1934) stated that the larva of *betulae* rolls a tube from the leaf-margin but in smaller leaves the whole leaf is rolled, although never into a spiral. In this respect he stated that the species resembles *P. sylvaticus* on *Sorbus*, which builds an (a) type roll. Stritt's (1936) description of the roll of *P. varius* Lep. (*vafer* L.) is that of type (a) and that of Malaise (1921) for *P. pallipes* corresponds to type (b). The young roll of *P. gyllenhali* was described by Conde (1934): this and those published and illustrated later by Stritt (1934, 1935) are type (b). I have also bred adults from both type (c) species.

Little difficulty has been experienced in rearing the larvae as these are robust and, when mature, quite powerful insects. It is preferable not to take them when very young as they suffer from the drying-out of the leaves: later this can be circumvented by placing fresh leaves close to the "feeding end" of the roll. These will be attached with silk to the roll, the characteristic shape in the type (b) being lost accordingly. Sometimes larvae of species of this type will leave their abodes and wander about—including up the wall of the jar—by means of the zig-zag silk bridge constructed as they move along (see p. 128). Type (c) larvae can detach their spire-like rolls from the parent leaf and move about—again even up smooth vertical surfaces —as if "walking on their hands," by means of their thoracic legs, eventually coming to rest and attaching the roll to a fresh leaf. On reaching maturity the larva leaves its roll and wanders rapidly about the bottom of the jar. Here no silk is used and the method of progression is quite different; the powerful mandibles are pressed backwards on the surface making an arch of the abdomen, which is then pushed forward in a sinuous movement, the thoracic legs and anal processes playing no part. A wide-mouthed 12 or 16 oz. bottle is filled with naturally damp sand and tapped down. For this I use the damp sand of lower greensand outcrops exposed by scraping away the dry surface layers, after removing stones, etc. Each larva is placed in a separate bottle to burrow. Under natural conditions it has been proved that *Pamphilius* larvae burrow to considerable depths of 40 cm. or so: in bottles they dig a maze of tunnels, with the sinuous action described, around the walls and within, until the sand is honeycombed, sometimes coming to rest, naked, in a visible position on the bottom. The bottle is capped tightly to prevent loss of water and stored in the dark during the winter. Using this technique my losses have been comparatively small, 44 sawflies and 12 parasites having been obtained from 68 larvae.

Species with type (a) larval abode.

Although *P. sylvaticus* L. is of wide distribution and is the species most frequently caught I have not yet found the larva for certain. Appearing

earlier than the other species, it flies from the first week in May until July in all types of localities, this, no doubt, being due to *Crataegus* being the host-plant most commonly selected, although several others have been recorded. The adults settle upon a wide range of plants, a habit which, as Stritt has remarked, in this genus gives no indication of the true host-plant. I found a roll upon *Crataegus* on 1st July, 1950, which, although I had no success in breeding the adult, was probably referable to this species and, at all events, serves to illustrate one form of the type (a) roll (Fig. 1). Here, although the larva was quite mature when found (fourteen days before feeding ceased) in this case there could be no possibility of the roll being originally a type (b) (see p. 135). One of the two basal lobes had been drawn over with silk attached to the upper side and brought flat against its opposite member, the margin not being rolled under and leaving only a narrow median channel within which the larva could retire. The remaining three free lobes of the leaf were eaten: the next stage would be either an attack upon the crude roll or upon neighbouring leaves pulled in towards it. The larva was of a deeper green than usual, with a pale brown head and yellow apex of the abdomen and terminal processes.

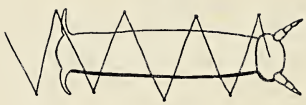
Species with type (b) larval abode.

Pamphilius gyllenhali Dahl. This species will be taken to illustrate the early stages, and the construction, of the roll.

On 19th June, 1949, I found two white, opaque *Pamphilius* eggs—recognized by their shape and glutinous covering—upon a leaf of *Salix atrocinerea* Brot., the third below the tip of a young twig, at Flitwick Moor, Beds. They were attached to the underside in the basal half upon either side of the midrib (Fig. 2). The twig was kept for observation in a bottle with the underside of the leaf outwards. At 8 p.m. on 21st June the "right-hand egg" was found to have hatched and the *left-hand* margin of the leaf already curled under by the larva into a roll 10 mm. long. One hour later the "left-hand egg" had hatched and the larva was already at the point A. Continuous progress was maintained by the characteristic *Pamphilius* method; with its back pressed to the leaf the larva laid a bridge of silk in a close zig-zag pattern along which it moved by means of the apical processes, little support apparently being provided by the thoracic legs (Fig. 2a). In attaching the silk to the leaf the larva—which is opaque white with a shining black head—stretches well out from the bridge and twists its head through a half-turn. Moving by the route shown, by 9.15 p.m. the larva reached the margin of the leaf at B, where, by leaning well over the leaf margin it attached threads to the upper, i.e. reverse, surface to points on either side of its position and then from each of these two points to the underside (facing the observer) near its anal end (Fig. 2b). This was continued for a short period, the larva then moved down the leaf margin—the supporting threads being attached to the latter but to the underside of the leaf—until a point C, about 10 mm. below B, was reached at 9.20. Here, still on its back with the head towards the base of the leaf, the larva laid a large number of cross-threads from the leaf margin to a region 2-3 mm. inwards from this, by swinging its head to and fro. This is evidently the main pad of tension threads and was worked at for 25 minutes. By 9.50 the edge of the leaf was beginning to curl inwards towards the under surface and the larva, having made a

Fig. 1

Fig. 2a.



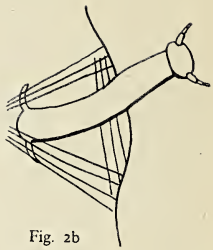


Fig. 2b

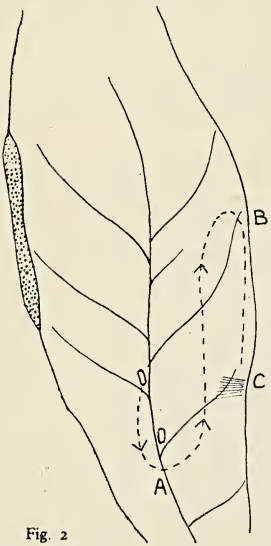


Fig. 2

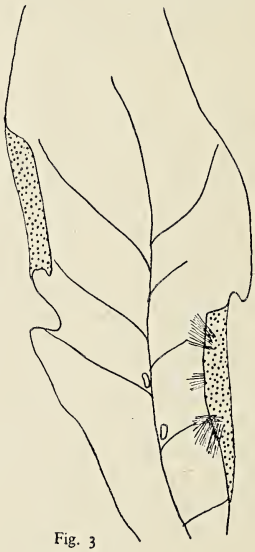


Fig. 3

PLATE I

Fig. 1. Type (a) roll upon *Crataegus* (slightly enlarged).

Figs. 2-3. Initial construction of type (b) roll of *P. gyllenhali* upon *Salix atrocinerea*: 2, showing path of freshly-hatched larva; 2a, showing method of progression of the larva; 2b, attachment of first threads at the leaf-margin; 3, appearance of completed rolls twenty-four hours after that shown in Fig. 2. Figs. 2a and 2b much enlarged, Figs. 2 and 3 slightly enlarged.

complete reversal in its position with ventral surface to the leaf and head towards the apex, appeared to be tightening the threads by arching its head or occasionally turning over on to its back and working the threads with its mandibles. At 10.10 the larva moved up beyond this pad of closely laid threads to a point between C and B and laid another pencil between a region on the under surface distant from the margin and the upper surface of the leaf on the incipient roll. Fifteen minutes later, the roll being still only a partially turned-in leaf margin, the larva nibbled the edge of the leaf between B and C above this second system of threads (those laid at B initially were evidently a "false start"), this being continued for four minutes, after which it retired to within the threads. This nibbling was not a meal as no ingestion took place, but served to break the leaf margin with the apparent result of helping the threads to pull the leaf into a roll. At 10.40 the larva turned round to make some more criss-cross threads at C, the roll still not being sufficiently closed to conceal it. My next observation was made at 12.20 a.m. when, although it had emerged over three hours previously, the larva still had not fed, but was laying a third set of threads below the other two, obliquely from the under surface of the leaf to the outside of the roll, which was then sufficiently well developed to conceal the larva. Fig. 3 shows the appearance of the rolls 24 hours after hatching.

The mechanism of roll formation is quite clear. Although this was only proved later with mature *latifrons* rolls, within a few minutes of being attached to the two surfaces of the leaf the threads contract, thus pulling the opposite side of the leaf over, a process assisted by the nick made in the leaf margin by the larva. This breaking of the margin is probably a general feature in the building of type (b) rolls as I have also observed it in the field in *betulae*. During the contraction the material of the threads draws up into small globules along their length, which, being permanent, enable a young or vacated *Pamphilius* roll to be distinguished from rolls made by lepidopterous larvae, etc., although these do not, of course, have the distinctive form of type (b).

Neither of the two larvae described above was raised to the adult, but there is no doubt as to their identity as *P. gyllenhali* adults were bred from rolls taken on the same willow tree. Three days after hatching, on the 24th, the larva whose progress had been observed left its roll and formed a new one at the apex of the leaf on the underside, but died two days later. The roll of the other larva on the "left hand" side of the leaf was large and well-developed on 26th June and, a head capsule having been pushed with frass through the outer end, the larva had passed into the second instar five days after hatching. It died in the same instar four days later. On another occasion I found two young rolls (and two empty egg-shells) upon the same leaf of *S. atrocinerea*, but, the larva being missing from one roll, I was unable to observe the outcome of the expected competition. Presumably one of the larvae would leave its roll and move to another leaf, but it is worth noting that in no other type (b) species have I found more than one egg or larva on one leaf.

The further development of the roll and feeding of the larva in this species is normal for the type as described later for *betulae* and *latifrons*, i.e., feeding takes place at the narrow proximal end and along the inner leading edge of the roll so that in section the latter, as a rule, only consists

of one complete involution. However—and so far this has not obtained with other host-plants—I have found rolls upon sallows in Bedfordshire and at Chamonix (Haute Savoie, August, 1951) consisting of several concentric involutions, which could only be achieved by the larva continuing to add pencils of threads at the proximal opening as soon as each set had fully contracted. Such rolls show a passage towards type (c). Possibly the softer texture of some sallow leaves allows this to be done.

The adults have been taken from the second week in May until early June, the larvae during June but, in the later season of 1951, a half-grown larva in a roll on *S. caprea* was found at the end of July. During 1949-50 I found larvae upon *S. atrocinerea* and *S. caprea* in three localities in Bedfordshire, and in all cases clearly defined type (b) rolls were constructed. In one case only has the complete development been followed: two rolls about three days old upon opposite surfaces of the same leaf of *S. atrocinerea* were found at Clophill on 5th June, 1949. When the leaf was gathered on the 17th one roll had been vacated at an early stage, the remaining larva ceased feeding on the 24th: total feeding period about three weeks. Pupation took place on 30th April, 1950, a female emerging 13 days later. Two further examples were bred on 18th May, 1950, and 27th May, 1951, pupal stages lasting no less than 11 days and no more than 22 days respectively. Parasites bred: two *Olesiocampe auctor* Grav.

Pamphilius latifrons Fallen. Little is known about this species and it has rarely been recorded from Britain. I first came across it on 22nd May, 1948, when I caught a female by hand on aspen at Flitwick Moor. She had just laid an egg which had become attached to her underside. The egg—unfortunately damaged—was 3 mm. long, curved, bright green and with a very glutinous covering. Nothing more of the species was seen during that summer. The following year on 9th July, while with Mr. Benson, I collected three type (b) rolls from the aspens in Bricket Wood, Herts. One of the larvae from these ceased feeding on the 27th and a male *P. latifrons* emerged from the bottle of sand on 27th May, 1950, this being the first recorded breeding of the species.

On 4th June, 1950, a female *latifrons* was observed settled upon one of a group of aspens at King's Wood, Heath and Reach, Beds. Mr. Benson has previously taken this sawfly at this spot but neither he nor I has found *P. betulae* in the district. I was therefore delighted to find, three weeks later on the 25th, a number of well developed and clearly defined type (b) rolls upon the sunward side of this group at a range of heights from the ground. Altogether eleven rolls were taken when first found or on 1st July and all the larvae were raised to the "burrowing" stage. It was not possible to make observations upon each roll as in some cases, the original leaves having partially died within a few days of gathering, the larvae left these and constructed atypical abodes among the fresh leaves provided. In four cases the egg had been laid upon the upper surface in positions near to the midrib, but the rolls were started by the larvae at different spots on the leaf margin and movement of three of them was in an anti-clockwise direction. Drawings of the rolls made on 26th June after the larvae had left them for fresh food illustrate these points (Fig. 4a-4d). In one example (see Fig. 4d) the empty egg-shell was hidden within the "feeding end" of the roll when gathered. Feeding and roll construction follows the characteristic pattern. Threads

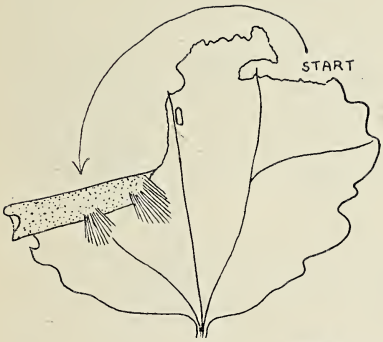


Fig. 4a

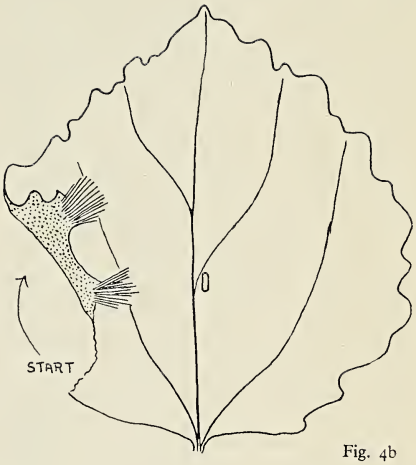


Fig. 4b

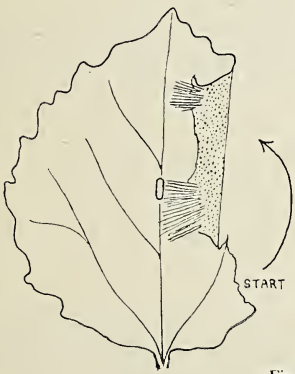


Fig. 4c

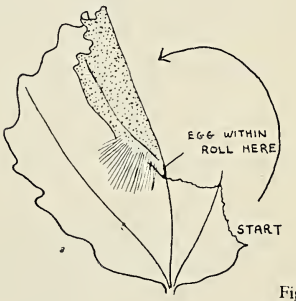


Fig. 4d

PLATE 2

Figs. 4a-d. Four rolls of *P. latifrons* upon *Populus tremula*, showing the construction of the type (b) roll and its movement around the leaf. Slightly reduced.

attached to the opposite surface of the leaf to that over which the roll will move and upon which the egg was laid contract and cause the leaf-margin to curl inwards, the transformation to a complete roll being effected by the contraction of further pencils of threads attached to spots still further over on the opposite (or under) surface of the leaf. Facing inwards the larva feeds upon the leaf immediately outside the (inner) narrow end of the roll. When all the leaf within reach has been eaten the larva feeds upon the curled-under or leading margin of the roll in sections at a time (Fig. 4b shows this), taking care to attach fresh pencils of threads to prevent the roll from opening out and to bring the feeding end round to fresh areas of the leaf-disc. In this way the outer marginal strip of the leaf is gradually brought into the roll and consumed with the greater part of the remainder of the leaf. As with *P. betulae* it is probable that one normal aspen leaf is sufficient for the full development of a single larva. The larval description was taken when feeding had ceased:

Head smooth, pale brown, in one example with darker brown areas on the hind orbits; antennae yellow; clypeus nearly white with three brown spots in a triangle above. Thoracic plate green, sometimes with faint brown smudges; there are no distinct lateral streaks above the legs, beneath a narrow black streak in front of the first pair. Abdomen green, caudal processes and apical margin yellow, the latter with yellow setae; sunken areas between the ribs of the anal segment green. Length 14-20 mm.

The larvae burrowed in the sand from 25th June to 10th July. Only one died during the following winter: from five of the larvae 1♂ 4♀♀ of a parasite *Homaspis subalpina* Schmied. emerged from 22nd-30th May, 1951, while five *P. latifrons* emerged as follows. Four of them having formed cells visible from without, were observed closely:

♂	pupated	23rd	April	emerged	16th	May	=	23	days	as pupa
♂	„	24th	„	„	13th	„	=	19	„	„
♂	„	26th	„	„	18th	„	=	22	„	„
♀	„	28th	„	„	21st	„	=	23	„	„
♀		—		„	21st	„		—		

Four of the parasitized larvae were visible in their cells and the parasite larvae were seen to have left their hosts and spun dark brown cocoons in the cells by 11th March, long before the *Pamphilius* larva would have pupated.

Pamphilius betulae L. (1) My first experience of this species was on 19th May, 1948, when I took a female on a leaf of a young aspen at Flitwick Moor, Beds. Ten days later, at the same locality, I found a blue-green *Pamphilius* egg stuck by its glutinous coat to the upper surface of a leaf near the base and to the left of the mid-rib. It was marked and kept under observation: by 10th June it had become slightly shorter and more rounded and on 12th the larva had emerged, evidently only a few hours previously when found, giving a duration of the egg stage of at least 14 days. The larva, which had not then taken a meal, had moved to the leaf margin (see Fig. 5a) and was attaching a second band of threads from the margin to the surface, a dense narrow band having already been laid lower down. Although not observed the subsequent movement can be inferred from the final appearance of the leaf after the completion of feeding shown with the roll

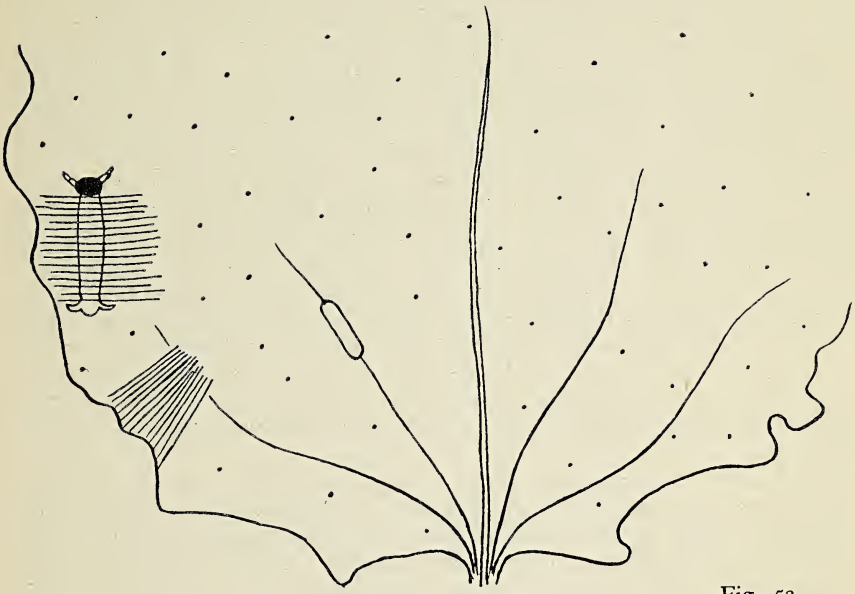


Fig. 5a

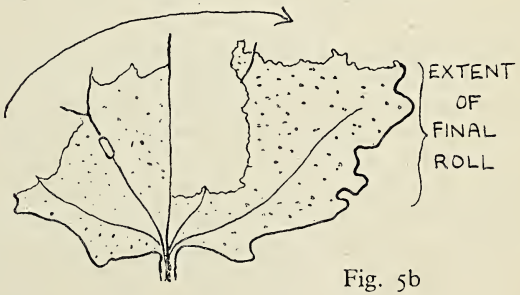


Fig. 5b

PLATE 3

Figs. 5a-b. *P. betulae* upon *Populus tremula*: 5a, leaf with egg-shell, freshly-hatched larva and initial mats of tension threads before their contraction has pulled the leaf-margin into the roll (much enlarged); 5b, remains of the same leaf after cessation of feeding, with the roll flattened out and showing its direction of movement (slightly enlarged).

flattened out in Fig. 5b. The larva must have reversed its position in the second web to face the base of the leaf then, as observed in the field seven days later, nibbled the margin between the two webs thus allowing the threads of the second web to pull the leaf into a roll as they contract. The roll then moved round the leaf in the direction shown. The larva was left on the tree until 25th June, the leaf removed and placed in a 4 oz. bottle with fresh aspen leaves. On 4th July the larva was placed on sand, pupated on 18th April, 1949, and a male *P. betulae* emerged on 3rd May.

(2) A second egg was found on the upper surface of a leaf in the same group of aspens on 12th June: this had not hatched by the 26th June, but, on 6th July when the leaf was removed, the larva was only a few days old as the initial roll had not moved. This larva ceased feeding on 26th July and again formed a cell within which it could be seen wriggling when the bottle was examined throughout the following winter. Pupation took place on 18th April, 1949, and a female *betulae* emerged on 7th May.

(3) A third larva in its initial roll—probably no more than two days old—was found on 26th June, gathered with its roll on 6th July and reared until 13th when feeding ceased. From this a male *betulae* emerged on 7th May, 1949.

(4) The following year two clearly defined, mature type (b) rolls with larvae on aspen were taken on 10th July at Flitwick. One of these ceased feeding five days later, a female *betulae* emerging on 13th May, 1950. The second entered diapause on 13th July, formed a cell on the bottom of the bottle and was examined daily from late March, 1950, onwards. Pupation took place on 12th April, a male *betulae* emerged on 7th May, the pupal stage thus lasting 25 days.

(5) Finally from several type (b) rolls collected from aspen, in company with Mr. Benson on 9th July, 1949, at Bricket Wood, Herts., one larva, which entered diapause on 25th July, gave a male on 11th May of the following year.

There is therefore no doubt that the larva of *P. betulae* constructs a type (b) roll. From the above breeding results the following summary of the biology of the species may be drawn. The adults emerge during May soon after the aspen leaves have expanded but still retain their immature brownish-red colour and are no more than about 40 mm. in length. As with other *Pamphilius* species they frequently interrupt their rapid flight and sun themselves on the leaves. The blue-green eggs are laid singly in any position upon the upper surface of the leaf—none have been found so far on the underside—being attached firmly by a glutinous secretion, and should be looked for during June. After a period of from two to three weeks the larva emerges: in the first instar it is about 5 mm. in length, pure white with shining black head. The larva, which is found up to the end of July, feeds for about three weeks in a type (b) roll, one leaf being sufficient. There are four feeding instars and a prepupal stage. Pupation takes place the following April, this stage lasting 15-25 days. In the prepupal stage at least, it is very similar to that of the previous species and, as both construct type (b) rolls there is no means, at present, of distinguishing *P. betulae* from *P. latifrons* in this stage.

Pamphilius pallipes Zett. and *P. varius* Lep. Both of these species are attached to *Betula*, *pallipes*—which with *P. sylvaticus* is one of the species

most frequently taken as the adult—outnumbering *varius* by about ten to one in Bedfordshire. During late May and June or even in July of 1948 rolls upon *Betula* were numerous; in fact I soon became accustomed to finding some after a few minutes search of any wood or roadside group of birch trees. In the case of *pallipes* most of the rolls were found upon a penultimate leaf of a short lateral twig, i.e., on the apical leaf at the time of oviposition, the egg being laid upon either surface near the midrib at the base of the leaf. Although the evidence from the appearance of the rolls when found was not clear-cut, I have no doubt that the type (b) roll is the characteristic form for both species.

Only upon three occasions have I bred *P. varius*, in each case from a type (b) roll from a different locality: (1) collected 19th June, 1948, ceased feeding 23rd June, adult 19th April, 1949; (2) collected 9th July, 1949, ceased feeding on 21st, adult 9th May, 1950, and (3) collected 6th August, 1949, when about four days old, ceased feeding 4th September to give an adult on 23rd June, 1950.

In addition to these, twenty-one rolls of various ages and stages of development have been collected from birch: of these fifteen taken during 1948 and one each in 1947 and 1949 gave adults of *pallipes*. The abode was recorded either as a clearly defined type (b) or as a more or less type (a) in those cases where either the leaf had one margin pulled over with threads without being completely closed into a roll or if several adjacent leaves or parts of leaves were strung together. An estimate of the relative ages of the rolls has been made by determining from the breeding data, the span in days, between the date of collection and the cessation of feeding, as follows:

type (b) rolls, 9, 10, 10, 11, 20, 20, 20, 23, 23.

± type (a) rolls, 6, 6, 7, 9, 9, 11, 13, 13.

Of those found which yielded no adults, the single type (a) had a residual span of 6 days whereas for the three type (b) rolls this period was 15, 15 and 28 days respectively. From these results it is evident that the type (b) rolls, when found, were, in general at an earlier stage of development than those of type (a). The most reasonable interpretation is that, in all cases, the roll made initially is of type (b) and, if the leaf is sufficiently large to provide food for complete development, the roll is continued in this clearly defined form until the larva ceases feeding. However, as the *Betula* leaf is small, in many cases to obtain sufficient food the larva will either "eat down" the roll when it has made the complete traverse of the leaf to give an open trough or will lean out, string together neighbouring leaves and feed on these, in both alternatives thus changing its abode to the type (a).

The life history of *P. pallipes* may be given in general terms as follows. The adults are found from the first week in May until the middle of June flying in the early morning and afternoon around birch and settling on the sunward side. The eggs are laid singly upon either surface of (usually) the apical leaf of a short lateral twig, but I have found as many as three rolls upon one short twig. In May, June or early July the rolls are to be found upon the hanging branches of fully grown trees or upon trees less than ten years old but most frequently on the side facing the sun. Initially they are of type (b), are constructed in the same manner as those of the aspen species

and of *gyllenhali* and move around the leaf in either direction; later the larva may consume almost the entire roll, thus obscuring its true form, or may obtain more food by attaching adjacent leaves to its abode. Three to four weeks are spent feeding and emergence of the adults takes place the following year after an extraordinarily short pupal period of from four to nine days. However, with two of a group of larvae collected in June, 1948, as no adults had emerged by the following June, the bottles containing them were tipped out to disclose two fresh and active larvae. They were replaced —one burrowed down and formed a cell adjacent to the wall on the bottom —and adults emerged on 9th and 27th May, 1950, respectively. This instance illustrates the robust character of *Pamphilius* larvae.

With *P. varius* the information is scantier, but, as stated above, in all three bred examples, the roll was a clearly defined type (b). Although I have taken a female in late May the evidence points to a later appearance than *pallipes*. The three authenticated rolls were found from late June to August and I swept a female (and a larva, from which a male *varius* emerged on 29th May, 1952) from birch at Rowney Warren, Beds., on 5th August, 1951.

The full-grown larva appears to be identical in the two species and very similar to, but smaller than, those of *betulae* and *latifrons*, i.e., the entire insect, including head, thoracic plates and anal segment, is green or yellowish-green, dark streaks sometimes being present above the thoracic legs. In the earlier instars the head is darker and in the penultimate, the anal segment, except the dorsal ribs, may be entirely black as in *P. histrio*. The only parasite bred from a larva from a type (b) roll on *Betula* is *Notopygus emarginatus* Holmgren, on 15th May, 1949, from a well-developed larva collected 13th June, 1948, at Dedmansey Wood, Whipsnade.

Species with type (c) larval abode.

The construction and development of this type of abode have been described by Stritt (1935) for *P. neglectus* Zadd.—a species not recorded from Britain—*P. histrio* Latr. and *P. inanitus* Vill.

Pamphilius histrio Latr. Three clearly defined type (c) rolls were found on 19th June, 1948, on the large, but typical, apical leaves of some aspen suckers at Flitwick Moor. In all these the egg had been laid upon the underside of the leaf, but the rolls, two of which were traversing the leaf in an anti-clockwise direction, had been started at different points on the margin as shown in Figs. 6a-6c drawn soon after the material was collected. The further development of the rolls could not be allowed to proceed as the larvae had to be preserved against the drying-out of the original leaf by feeding with fresh leaves placed close to the abode. Feeding ceased on 6th, 6th and 14th July respectively and all three burrowed to rest visibly in cells on the bottom of the bottles of sand. Pupation took place on the same day, 24th April, 1949, and all three females emerged, curiously enough, nineteen days later upon 13th May.

A fourth example was taken in the same locality on 17th July, 1948. This was at first recorded as a type (b) roll as it consisted of the basal part of a small aspen leaf drawn into a tight roll. However, on opening the roll the following day, after the larva had left to enter diapause, it was found to contain a narrow outer strip of dead, dried leaf, twisted into a screw and

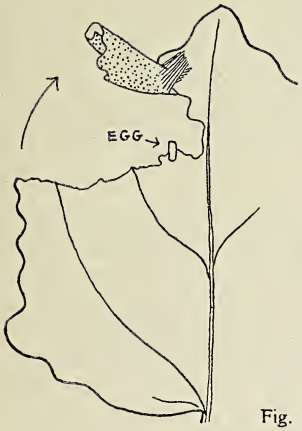


Fig. 6a

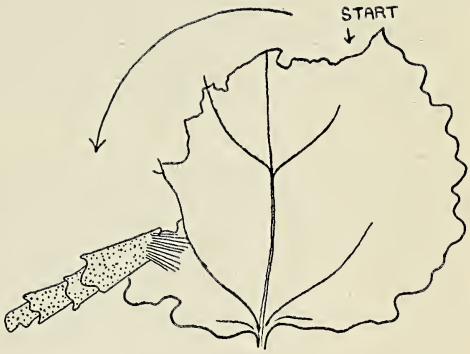


Fig. 6b

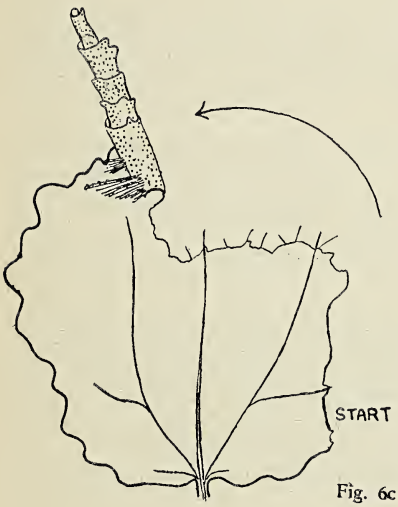


Fig. 6c

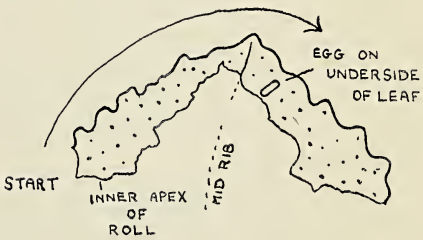


Fig. 7

PLATE 4

Figs. 6-7. Type (c) roll of *P. histrio* upon *Populus tremula*: 6a-c, three individual rolls at different positions in their travel over the underside of the leaf; 7, a complete roll, unrolled to show its construction from a marginal strip and direction of movement. All about natural size.

tied with silk within one end of the roll. This was evidently the outer end of the original type (c) roll which the larva, having eaten the original leaf, carried with it to complete its feeding upon the new leaf, the latter being rolled into a single involution resembling the normal type (b) abode. Care is needed to diagnose correctly abnormal rolls like this resulting from a change of pabulum—as in the birch species—but the dead piece of marginal strip of leaf gave the clue. This larva also overwintered visibly in a horizontal position in its cell, pupation took place on 25th April, 1949, and a male *histrio* emerged nineteen days later.

Two more early type (c) rolls were found on aspen on 20th and 23rd June, 1948, at Dedmansey Wood. As it was discovered later, in both cases the egg was laid upon the underside towards the apex of the leaf. In the second example, after hatching, the larva must have crawled over on to the upperside as the roll was near the base of the leaf on that side and moving towards the petiole. Later, when these two rolls were collected on 30th, this roll had reversed and was moving in the opposite direction, subsequent development being impossible to observe for the usual reason, especially in this case as the leaf was too small for the total needs of the larva. The movement in a clockwise direction—viewing the leaf from the underside—of the other roll was shown by unrolling to give the original marginal strip—and revealing the egg-shell—as shown in Fig. 7. This larva ceased feeding upon 18th July, resting in a cell visible outside until 10th April of the following year. On 15th, i.e., a few days before the normal pupation date, an hymenopterous parasite larva had emerged and built a brown cocoon. From both bottles examples of *Olesiocampe auctor* Gravenhorst emerged on 14th and 15th May respectively.

Lastly, two type (c) rolls upon aspen were collected during a visit with Mr. Benson to Bricket Wood, Herts., on 9th July, 1949. These ceased feeding towards the end of the month and produced two male *histrio* (one of which is now in the British Museum (Nat. History) collection) on 21st and 18th May, 1950, respectively, one of them spending fourteen days in the pupal stage.

The last instar is similar to that of *betulae* and *latifrons*, but, as observed by Stritt (1935), unlike these two species, the anal segment of the abdomen has black sunken areas between the ribs and is entirely black beneath, with black hairs on the margin. The thoracic plate is black or brown medially and there are well-marked black streaks or plates above and anteriorly to the thoracic legs and ventrally between the second and third pair.

The adults and larvae of all three aspen species are found during the same period of the early summer.

Pamphilius inanitus Vill., the remaining species with a type (c) roll is found upon native and cultivated species of *Rosa*, the adults flying in late May and June. During July, 1950, I took three rolls upon rose in the Whipsnade and Studham area of Bedfordshire, from two of which I obtained females on 22nd May, 1951, one of which spent twenty-one days as a pupa, the third larva surviving until 24th April. In the last instar these larvae varied from entirely green without trace of dark colour to a condition resembling that described above for *histrio* with black anal segment, black streaks above the thoracic legs and additional black transverse lines between the abdominal segments beneath.

Discussion.

After considering the available information upon the roll types of *Pamphilius* species I conclude that basically there are two, i.e., (c) and (b) respectively. Stritt's original definition of these applies, but the essential difference is that type (c) is constructed from a narrow marginal strip of the leaf which, as it is at no time consumed by the larva, gradually withers; whereas in type (b) the roll, constructed from a wide marginal strip is progressively eaten as it moves round the leaf, the unrolled part of the leaf also being eaten, as by type (c) larvae.

This distinction is clearly seen in relation to different size of leaf of the host-plant species. Of those that construct type (c) rolls, in the following species the leaves of their host-plants are large, one leaf being, in general, sufficient for one larva, the roll accordingly is constructed entirely from the margin of and remains attached to, the original leaf: *histrio* (aspen), *neglectus* Zadd. (sycamore; non-British) and *marginatus* Lep. (hazel, hornbeam; non-British). In the rose species *inanitus*, however, where the leaflets are small, the larva obtains sufficient food by moving and attaching its roll to the margin of a fresh leaf which is incorporated therein. As I have already pointed out movement to another leaf may take place in *histrio* if the original leaf is too small.

The majority of the type (b) species feed upon plants having large leaves and in these the roll is clear and well developed: *betulae* and *latifrons* (aspen), *gyllenhali* (*Salix caprea*, *atrocinerea*), *hortorum* (*Rubus*), *vafer* (alder), *fumipennis* (hazel). If, however, the original leaf selected by any of these species is a small example or, as in the birch species *varius* and *pallipes*, the host-plant normally has small leaves, when the leaf outside the roll has been eaten, unlike the type (c) larva upon small leaves, the larva does not move but eats down the roll or strings together adjacent leaves, effecting a change to Stritt's type (a). In other words the building of a type (a) roll is a response to size of leaf. It should be noted that the two type (a) species *stramineipes* Hartig (Stritt, 1934) and *sylvaticus* both feed upon small-leaved plants: the former upon rose and the latter, a polyphagous species, has been recorded upon mountain ash, hawthorn, blackthorn, domestic plum and *Prunus padus* L. Whether there is a definite type (a) roll could be determined, for example, by placing a freshly hatched larva of *sylvaticus* upon a large plum leaf and noticing its reaction. The crucial difference between type (a) and types (b) and (c) would be shown in the early stage of the roll as in both the latter a nick is made in the leaf-margin by the larva after laying the first mat of tension threads to make the rolling of a separate strip possible, whereas in a type (a) roll this would not be done, the threads —which would also be longer—merely pull together parts of the leaf.

It would also appear from Stritt's drawings (Stritt, 1935, p. 144) that sometimes the roll is not consumed by the larva of *gyllenhali* and *hortorum*, but eventually consists of several involutions. As stated earlier (p.130) I have also seen this type rarely in a *Salix* species. This shows some passage to type (c) except that the roll is quite differently constructed.

Finally, the egg may be laid upon either surface of the leaf, although I have not yet found a *histrio* egg upon the underside of aspen. More significantly the eggs appear to be laid more or less aligned with the axis of the

leaf: this may be due to the female taking up a lengthwise position for ovipositing. In both types (b) and (c) the roll may move in either direction around the leaf in a given species and the position of the egg has no influence upon this as the larva wanders before starting its roll.

The parasites bred from *Pamphilius* larvae were kindly determined by Mr. J. F. Perkins of the British Museum (Natural History), in which collection they have been deposited.

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Printed by SYDENHAM & Co. (Est. 1840) LTD., Printers, Oxford Road, Bournemouth